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A review of the ecological value of Cusuco National Park: an urgent call for conservation action in a highly threatened Mesoamerican cloud forest.

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Abstract

Cloud forests are amongst the most biologically unique, yet threatened, ecosystems in Mesoamerica. We summarize the ecological value and conservation status of a well-studied cloud forest site: Cusuco National Park (CNP), a 23,440 ha protected area in the Merendón mountains, northwest Honduras. We show CNP to have exceptional biodiversity; of 966 taxa identified to a species-level to date, 362 (37.5%) are Mesoamerican endemics, 67 are red-listed by the IUCN, and at least 49 are micro-endemics known only from the Merendón range. CNP also provides key ecosystem services including provision of drinking water and downstream flood mitigation, as well as carbon sequestration, with an estimated stock of 3.5 million megagrams of carbon made in 2000. Despite its ecological importance, CNP faces multiple environmental threats and associated stresses, including deforestation (1,759 ha since 2000 equating to 7% of total forest area), poaching (7% loss of mammal relative abundance per year), amphibian declines due to chytridiomycosis (70% of species threatened or near-threatened), and climate change (a mean 2.6 °C increase in temperature and 112 mm decrease in rainfall by 2100). Despite conservation actions, including community ranger patrols, captive-breeding programmes, and ecotourism initiatives, environmental degradation of CNP continues. Further action is urgently required, including reinforcement and expansion of ranger programmes, greater stakeholder engagement, community education programmes, development of alternative livelihood projects, and legislative enforcement and prosecution. Without a thorough and rapid response to understand and mitigate illegal activities, the extirpation and extinction of species and the loss of vital ecosystem services are inevitable in the coming decades.

Resumen extendido

Antecedentes: Los bosques nublados se encuentran entre los ecosistemas con mayor singularidad de biodiversidad, pero también entre los más amenazados en Mesoamérica. A pesar de esto, son raros los estudios de casos explícitos que resumen el valor ecológico particular de los bosques nublados, al igual que información sobre las amenazas que enfrentan y la efectividad de las intervenciones de conservación empleadas en ellos. Aquí resumimos el valor ecológico y el estado de conservación de un bosque nublado ampliamente estudiado: el Parque Nacional Cusuco, un área natural protegida de 23,440 ha ubicada en la cordillera del Merendón al noroeste de Honduras.

Métodos: Resumimos datos de más de cien publicaciones científicas, así como datos de varias fuentes inéditas, con el objetivo de proporcionar un resumen exhaustivo del valor ecológico del Parque Nacional Cusuco, las amenazas que enfrenta y el éxito de las intervenciones de conservación empleadas en el parque hasta la fecha. La mayoría de la información revisada proviene de los muestreos realizados por Operación Wallacea, que han sido efectuados estacionalmente en el parque en los últimos quince años. No obstante, se revisaron muchas otras fuentes de información, algunas de las cuales se remontan a la década de los ochenta.

Resultados: Demostramos que el Parque Nacional Cusuco tiene un valor excepcional de conservación, alberga por lo menos 327 especies de árboles y arbustos, 470 especies de vertebrados, y una diversidad de comunidades de artrópodos. Esto incluye 67 especies clasificadas globalmente como amenazadas y casi amenazadas, así como por lo menos 49 especies reconocidas como microendémicas para la región de la cordillera del Merendón. El parque proporciona servicios ecosistémicos claves, como la provisión de agua potable y la mitigación de inundaciones, el secuestro de carbono, con un stock estimado de 3,5 millones de megagramos de carbono generado en el año 2000.

A pesar de su gran importancia, el Parque Nacional Cusuco enfrenta múltiples peligros ambientales, incluyendo la deforestación (1,759 ha desde el año 2000, equivalente al 7% del área forestal total), caza ilegal (pérdida del 7% de la abundancia relativa de mamíferos por año), disminución de la población de anfibios por quitridiomicosis (70% de las especies catalogadas como amenazadas o casi amenazadas), y el cambio climático (un aumento promedio de 2.6 °C en la temperatura y una disminución de 112 mm en la precipitación durante el 2010). Las acciones de conservación que han sido implementadas incluyen patrullas comunitarias de guardaparques, programas de cría en cautividad *ex situ* e iniciativas de ecoturismo.

Discusión: A pesar de las acciones de conservación implementadas hasta la fecha, la degradación ambiental en el Parque Nacional Cusuco aún continúa. Se requieren medidas adicionales con urgencia, estas medidas incluyen incrementar el refuerzo y expansión de los programas de guardaparques, un mayor compromiso de las partes involucradas, programas de educación comunitaria, desarrollo de proyectos de estrategias alternativas de subsistencia para las comunidades, así como la aplicación y enjuiciamiento legislativo. Sin una respuesta rápida y exhaustiva para comprender y mitigar las actividades ilegales en el parque, serán inevitables las extirpaciones, extinciones de especies y la pérdida de servicios vitales del ecosistema en las próximas décadas.

Introduction

Tropical montane cloud forests ('bosque nublado') are broadly defined as "tropical forests frequently covered in cloud or mist" (Stadtmuller 1987). They are geographically restricted, comprising between 2.5% (Cayuela *et al.* 2006a) and 14.2% (Mulligan 2010) of forest ecosystems worldwide, depending on the definition used. The term 'cloud forest' can apply specifically to 'upper montane rain forest' (as defined e.g. by Richards 1996), but as other sources, in this review we use the term in a broader sense which includes a range of broadleaved montane rain forest types. Cloud forests are ecologically unique and support a high diversity of flora and fauna (e.g. Leo 1995; Long 1995). They are centres of endemism for plants (Bubb *et al.*

2004), invertebrates (Anderson & Ashe 2000), and herpetofauna (Wilson & McCranie 2004) and provide habitats for 10% of all range-restricted bird species (Stattersfield *et al.* 1998). As such, they are disproportionately well-represented within global biodiversity hotspots (Myers *et al.* 2000; Brooks *et al.* 2006) and "irreplaceable" protected areas (Le Saout *et al.* 2013). Cloud forests also provide a wide range of ecosystem services, including water catchment protection (water filtration and storage, and downstream flood mitigation), carbon sequestration and storage, nutrient cycling, and biodiversity mediated services such as adjacent crop pollination, soil aeration, waste removal, and pest biocontrol (Bubb *et al.* 2004; Martinez *et al.* 2009).

The Mesoamerican biodiversity hotspot (Myers *et al.* 2000) is particularly rich in cloud forests. Despite their well-recognized ecological importance (Rahbek *et al.* 2019), Mesoamerican cloud forests are critically threatened ecosystems, experiencing high rates of habitat loss (Cayuela *et al.* 2006b). For much of the early and mid-twentieth century the integrity of these forests remained relatively intact due to their inaccessible nature. However, in recent decades human population growth, mechanization of forestry activities, and improved accessibility have resulted in an increase in cloud forest deforestation and habitat degradation (Aldrich *et al.* 1997; Powell & Palminteri 2001; Hansen *et al.* 2020). They are also disproportionately threatened by the impacts of amphibian diseases (Scheele *et al.* 2019) and global climate change (Feeley *et al.* 2011; Fadrique *et al.* 2018).

Despite representing an urgent conservation priority (Bubb *et al.* 2004), detailed, cross-disciplinary case studies documenting specific sites remain scarce and geographically localized. While some sites in South America and southern Mesoamerica have been relatively well-studied (e.g. Leo 1995; Nadkarni & Wheelwright 2014), there is a paucity of research within northern Mesoamerican cloud forests. Most existing research from the region has focussed on Guatemala and Mexico (e.g. Renner *et al.* 2006; Martinez *et al.* 2009) and tend to be individual studies rather than the products of long-term multi-disciplinary research. Similarly, while conservation strategies to protect remaining areas of these northern Mesoamerican cloud forests have been proposed (e.g. Toledo-Aceves *et al.* 2011), few publications have evaluated the successes of these strategies.

Cusuco National Park (hereafter CNP or 'the Park'), located in the Departments of Cortés and Santa Bárbara, northwest Honduras (Fig. 1), is one of several protected areas within the Cordillera del Merendón (hereafter the Merendón range). To the best of the authors' knowledge, it is the most intensively studied site within these mountains, and possibly within

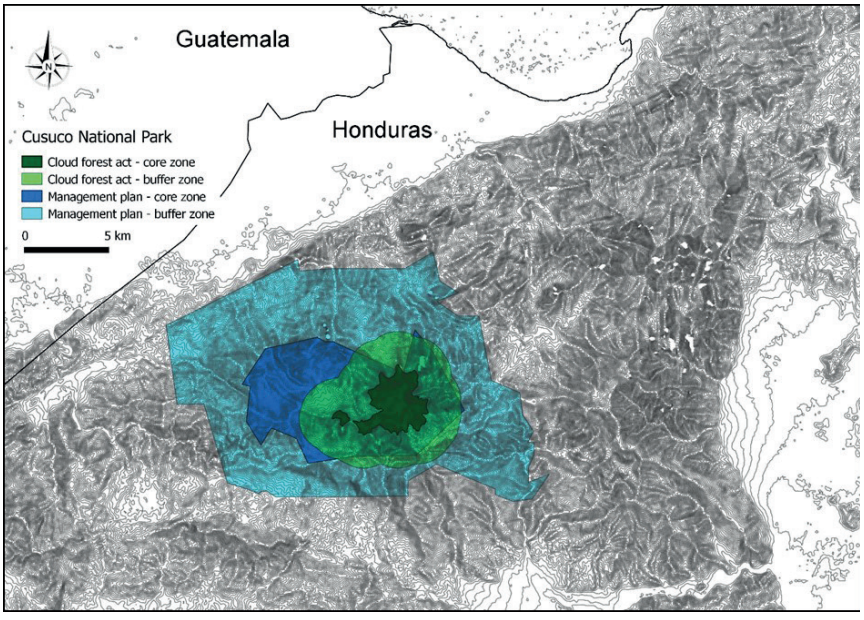

Fig. 1. Boundaries of Cusuco National Park, north-west Honduras, as defined by the Cloud Forest Act (1987) and the Park's Management Plan (1994).

northern Mesoamerican cloud forests generally. This is due to the long-term, annual, multi-taxa biodiversity monitoring programme run by the UK-based expedition company Operation Wallacea (Opwall). This programme has been run in collaboration with the Instituto de Conservación Forestal (ICF) and academic partners worldwide. Surveys to date have consisted of an annual eight-week field season (June–August) between 2004 and 2019 (and occasionally interspersed with more specific fieldwork at other times of year), where most data have been collected along a network of permanent transects radiating from seven temporary forest camps (Fig. 2). While baseline biodiversity surveys and systematic monitoring efforts have been the primary focus of these expeditions, specific work has also been undertaken to quantify ecosystem services and identify and monitor environmental threats. This has allowed for the development of strategies for local conservation interventions. In addition to the Operation Wallacea programme, other organisations and individual scientists have also conducted research in CNP (particularly with regards to its herpetofauna which has been the subject of surveys since the 1980s – see McCranie & Wilson 1981). As such, CNP is well represented in the scientific literature, with 107 peer-reviewed scientific papers, three books/book chapters, and eight PhD theses all using primary data sourced from the Park published to date (see Supplementary Appendix SS1). These encompass fields as diverse as methodological survey and experimental design (Caras & Korine 2009; Martin *et al.* 2010; Erzberger *et al.* 2011; O'Callaghan &

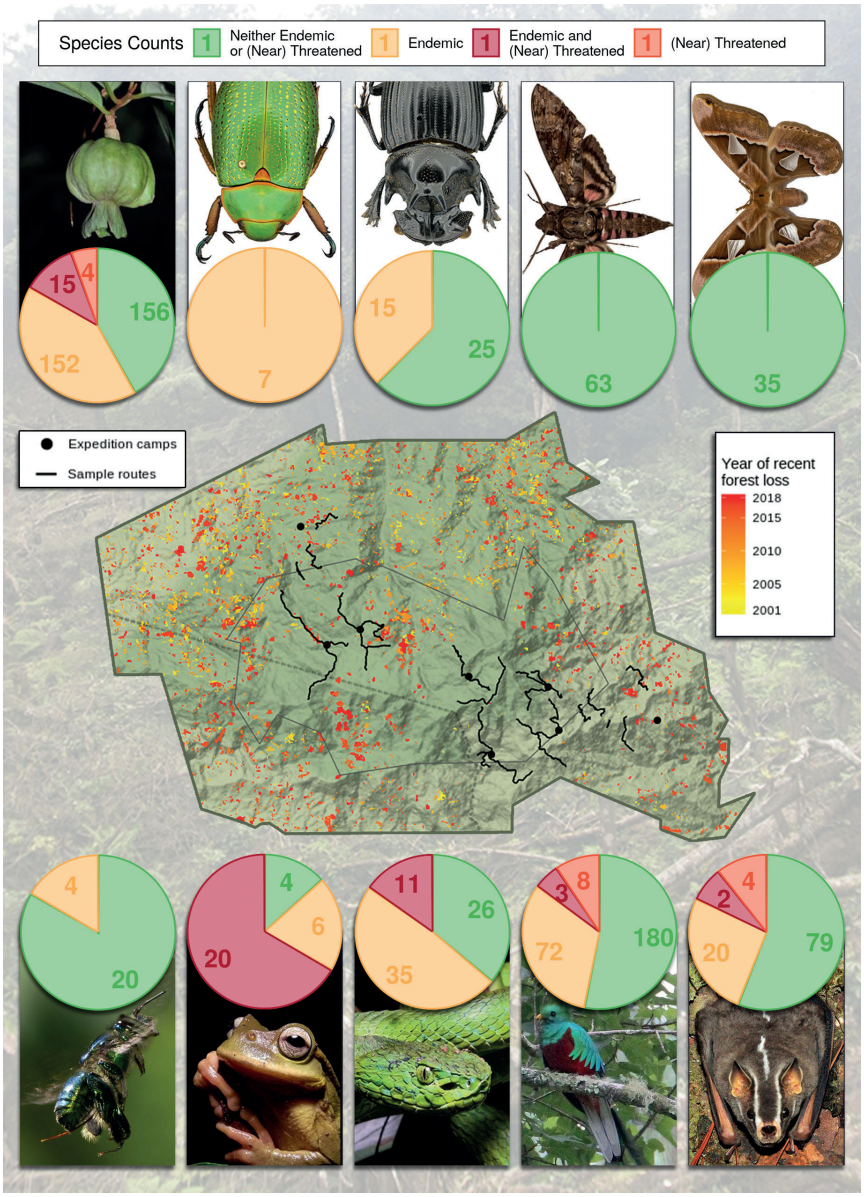

Fig. 2. A graphical overview of biodiversity, survey sites, and forest loss in Cusuco National Park. Centre: the scale of recent forest loss in CNP up to 2018. Areas not on the yellow-red spectrum have not undergone forest loss or were lost prior to 2000. The core zone of the park is denoted by the inner grey line, and the Operation Wallacea expedition sampling network shown by black points (camps) and lines (sample routes). Pie charts summarize data on taxa surveyed intensively in CNP. These are (top row): trees and shrubs, Chrysina jewel scarabs, Scarabaeinae dung beetles, Sphingid moths, Saturnid moths, (bottom row) Orchid bees, Amphibians, Reptiles, Birds, Mammals. Pie chart segments show numbers of species that are endemic to Mesoamerica (cream), threatened / near-threatened (red), endemic and threatened / near-threatened (magenta) and not endemic or threatened (green). All photos are copyright to authors or author institutions. Basemap by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

Kelly-Quinn 2012; Albergoni *et al.* 2016; Martin *et al.* 2017; McCravy *et al.* 2017), species descriptions (Lorence *et al.* 2015; Rodrigues *et al.* 2017), species inventories (Hoskins *et al.* 2018), ecology and behaviour (Jones *et al.* 2020a), comparative physiology (Jones *et al.* 2020b), population genetics (Asher 2009; Bunting *et al.* 2016), applied conservation (McCann *et al.* 2012), species community responses to environmental change (Neate-Clegg *et al.* 2018), species-specific zoological studies for invertebrates (Stanbrook *et al.* 2017; Lonsdale & Brown 2019), fish (Olinger *et al.* 2016) and herpetofauna (Talley *et al.* 2005; Wilson *et al.* 2006; Hess *et al.* 2015; Clause & Brown 2017; Arrivillaga & Brown 2018; Brown & Arrivillaga 2018; Brown *et al.* 2018; Brown 2018, 2019, 2020; Brown *et al.* 2020; Lonsdale *et al.* 2020; Sasso *et al.* 2020), and contributions to global-scale macro-ecological studies (e.g. Cayuela *et al.* 2012; Crowther *et al.* 2015; Slik *et al.* 2015, 2018; Mendieta-Leiva *et al.* 2020).

We present a synthesis of research undertaken in CNP to date based on both annual field seasons (methodologies summarised in Gilroy *et al.* 2017) and findings from additional studies. First, we summarise the history, general ecology and ecosystems of CNP, and then specifically summarise and describe data on species richness, endemism, and threatened species for each major taxonomic group. We then assess ecosystem threats, the efficacy of conservation interventions, and finally, highlight further conservation actions necessary for the long-term preservation of CNP. We intend this review to represent a 'call to arms' for the better protection of CNP specifically, and Neotropical cloud forests generally.

1. Study site

CNP occupies the central portion of the Sierra Omoa, one of several smaller mountain chains that together comprise the Merendón range. The Park spans an elevational range of 500–2,242 m a.s.l (ICF 2015) (Fig. 1) and was established after the passing of the Cloud Forest Act (Act 87-1987) as part of the Sistema Nacional de Áreas Protegidas de Honduras (SINAPH) (Bonta 2005; Martin & Blackburn 2009). It was principally created to protect the watershed that supplies the second-largest city in Honduras, San Pedro Sula (population ~700,000), and the densely populated Sula Valley (Townsend & Wilson 2008). Similar watershed protection outcomes were also the main reason for the establishment of most other cloud forest national parks during this period (Cruz 1993).

The Park is adjacent to three other protected areas, including two forest regions protected under Act 53-1959 (Zona Forestal No2) and Act 210-1985, and a Water Protection Zone (Act 46-1990). The Park originally consisted of a core zone delineated as all terrain >1,800 m a.s.l and a surrounding 2 km buffer zone (Fig. 1). In 1991, the management responsibilities of CNP were passed from the Dirección General de Recursos Naturales Renovables (RENARE) to the Corporación Hondureña de Desarrollo Forestal (COHDEFOR). Following this, in 1994 a park management plan was published by COHDEFOR covering 23,440 ha which recommended an extension of the core zone to 7,690 ha, within which permanent settlements and any activities involving extraction of forestry resources were not permitted. The plan also advocated an extension of the buffer zone to 15,750 ha, within which some limited land use was permitted (Fig. 1). However, these proposed management plan boundaries have never been officially recognised by the Honduran government, and thus some uncertainty and controversy remain over the precise position of the Park's boundaries. Land use zonation is further complicated by the disputed ownership of some land parcels within the Park (H. Hoskins *pers. obvs.*).

2. Ecological significance

2.1. Environmental conditions and vegetation types

The Merendón range was formed by a Palaeozoic granitic intrusion into volcanic ash sediments (Williams 2006). This granite is only exposed in riverbeds above 1,450 m a.s.l; elsewhere the surface geology is dominated by strata of gneiss and schist (Williams 2006). The terrain is rugged, with steep slopes, narrow ridges and deep valleys. Soils are strongly acidic throughout forested areas, with pH ranging from 3.0 to 4.5 in the top 5 cm (F. Brearley, *unpubl. data*). Total annual precipitation is *ca.* 3,000 mm with 45% of rainfall falling in the wettest months between October and December (Fundación Ecologista 1994). Mean day time temperatures in summer (June–July) range from 21 °C at 1,150 m a.s.l (range: 18 °C – 23.5 °C) to 15 °C at 2,200 m a.s.l (13 °C – 16.5 °C) (Jones 2020), with adiabatic lapse rates of 5–6 °C/1000 m (typical of tropical mountains e.g. Freeman 2015).

The upper and middle elevational ranges of the Park (*c.* 1300 m – 2242 m a.s.l) are largely covered with closed canopy forest, much of which has experienced little anthropogenic disturbance, although patches of deforestation have begun to appear in recent years and are increasing annually. There are also extensive areas of secondary forest at various stages of successional development, mostly below 1,300 m a.s.l. Older stands of secondary forest are the result of historical commercial logging, which occurred from the 1950s to the 1980s. Younger stands occur partly due to more recent illegal deforestation and disturbance, and partly due to storm damage (Batke & Kelly 2015).

Most of the forest is dominated by a heterogenous community of broadleaved evergreen trees, with no single dominant species. From approximately 1,300–1,800 m a.s.l, in the Park's core zone, relatively intact lower montane rain forest predominates, interspersed with patches of secondary forest. The best-developed stands contain such characteristic lowland tropical elements as custard-apple family (Annonaceae) and strangler figs (*Ficus* spp.). Gaps in the forest canopy are quickly colonised by the fast-growing pioneer 'guarumo' or trumpet tree (*Cecropia peltata*). Characteristic trees across a range of elevations include oaks (*Quercus* – at least nine species), a large number of species in the laurel family (Lauraceae), and sweet gum (*Liquidambar styraciflua*), which is one of the few deciduous species and one of the tallest-growing trees in CNP, exceeding 60m in some locations. The forest understorey is largely dominated by tree-ferns, dwarf palms, and locally bamboos, along with a wide diversity of shrubs and smaller trees.

Areas of pine forest occur in CNP, particularly on the drier eastern slopes, and are notably less diverse than the broadleaved forest. Pine forest canopy is dominated by *Pinus maximinoi* (Maximino's pine, found in both primary and secondary forest across a range of elevations) and *P. tecunumanii* (Schwerdtfeger's pine, largely in secondary forest at lower elevations). Pines, oaks, and sweet gum all belong to the 'northern' biogeographical elements in the forest flora that are approaching their southerly range limits in Honduras.

With increasing elevation, the cooler temperatures and higher rainfall bring about a transition to upper montane rain forest ('true' cloud forest in a narrower sense) at approximately 1,800 m a.s.l. Community composition of trees here alters, but the most striking change is in the increasingly luxuriant growth of epiphytes. This vegetation zone is characterised by thick growths of mosses, liverworts, ferns, bromeliads, and orchids. At altitudes >2,000 m a.s.l, on exposed mountain peaks and ridge tops, elfin forest (*'bosque enano'*) occurs. Vegetation here is of low stature, comprising a densely interwoven canopy of small trees and shrubs, and with epiphytes growing right down to ground level. The topsoil is a spongy humus, the result of lower decomposition rates combined with intense leaching.

Concerning terminology: '*bosque enano*' (elfin forest) is widely used to refer to dwarf, moist, high-altitude forest/scrub. However, Mejía-Valdivieso (2001) differentiates between '*bosque musgoso*' (mossy forest)/'*bosque hepática*' ('hepatic forest'), which he records from the Cerro Jilinco area of CNP, and an even more stunted vegetation type that he denotes as true '*bosque enano*/dwarf forest', and records only from the Sierra Agalta.

A high abundance and diversity of epiphytes – plants which start life perched on a tree trunk or branch – is a characteristic feature of cloud forests (Bubb *et al.* 2004). Epiphytes are very common throughout CNP (Batke *et al.* 2016), with the highest diversity being found in mid- and upper-elevation forest. These include holoepiphytes (which have no contact with the ground at any part of their lifecycle) and hemiepiphytes (which develop on another plant and send aerial roots towards the soil, allowing some to become large shrubs or even trees) (Moffett 2000). Holoepiphytes in CNP include orchids, ferns, and bromeliads, with a single tree able to host as many as 37 species (S. Batke, *unpubl. data*). Bromeliads are particularly conspicuous, with genera such as *Werauhia*, *Catopsis*, *Vriesea* and *Tillandsia* containing an 'aerial pond' or phytotelma (plural phytotelmata) at the centre of each leaf rosette; the associated fauna of which is of special interest to zoologists (see below). Hemiepiphytes also occur throughout, *Clusia* spp. being the most plentiful. The second major group of 'hangers-on' are the climbers *sensu lato* – plants which start life at ground level and then climb up the tree towards light. These may be subdivided into climbers *sensu stricto*, in which the plant remains rooted at the base and is hence stationary throughout its lifetime, and nomadic vines, which send out adventitious roots as they grow, allowing the plant as a whole to shift position in the course of its lifetime (Moffett 2000). In CNP, nomadic vines in the arum family (Araceae) are plentiful, notably the genera *Philodendron* and *Monstera*. The final group are the mistletoes which, unlike true epiphytes, are hemiparasitic, extracting water and dissolved nutrients from the xylem of the host tree.

The buffer zone, which surrounds the core zone in all directions at lower elevations, is composed of a mosaic of secondary forest, cropland, coffee plantations, and pasture for cattle, and includes 12 villages with a combined population of 3,082 (Honduran 2014 census data - https://www.ine.gob.hn/V3/).

The most abundant aquatic habitats in CNP are its network of rivers and streams. The Park has very few standing waterbodies. Most of these are artificial ponds in the vicinity of villages in the buffer zone, including small ponds maintained for fish cultivation. Besides rivers, the most common aquatic habitats are phytotelmata and water-filled tree holes.

2.2. Biodiversity

A compilation of survey data from Opwall (following methodologies summarized in Gilroy *et al.* 2017), along with other previously published data, indicates that 966 taxa have been identified to species-level in CNP to date, including 362 Mesoamerican endemics (37.5% of all species) and 67 threatened or near threatened species (including nine Critically Endangered species), with a further three species being listed as Data Deficient (Table 2). A total of 49 species (six plants, 21 arthropods, 22 vertebrates) are micro-endemics known only from the Merendón range (Table 3). We summarize key findings relating to diversity, endemism, and threat status of different taxa visually in Fig. 2. as well as in the sections below:

Plants

The flora of CNP is diverse and supports many rare and little-known species. A total of 913 vascular plant species have been recorded to at least a morphospecies level from forested areas >500 m a.s.l. Of these, 49.4% are trees and shrubs, 22.1% epiphytes, 17.2% terrestrial herbs, 9.9% climbers and 1.4% mistletoes. Of the total, to date 78% have been identified to species-level, 15.4% to genus, 4.6% to family and 2% only as 'morphospecies' (D. Kelly & S. Batke, *unpubl. data*).

Taxonomic inventory work completed to date has focussed on the trees and shrubs, which constitute the 'framework' of the forest ecosystem. Of the 327 trees and shrubs identified to species-level, 167 (51.1%) are endemic to the Mesoamerican biodiversity hotspot (Table 1) and 19 (5.8%) are IUCN-listed as threatened or near threatened (Table 2). The list of micro-endemics includes three trees, two shrubs (dwarf palms; Hodel *et al.* 1995), and one herb (Table 3). Four of these species are newly described: *Hondurodendron urceolatum* ('Honduras Tree', Ulloa Ulloa *et al.* 2010), *Sommera cusucoana* ('Cusuco Coffee Tree', family Rubiaceae; Lorence *et al.* 2015), *Styrax paulhousei* ('Paul House's Snowbell Tree', family Styracaceae;

Fritsch *et al.* 2018) and *Calathea carolineae* ('Caroline's calathea', family Marantaceae; Kennedy 2012). The discovery of *Hondurodendron* is particularly remarkable. A monotypic genus, it appears to be a palaeoendemic, its evolutionary isolation likely dating back to the period when the land that is now northern Honduras was an outpost at the southernmost tip of the North American continent (Montes *et al.* 2015). Three of these new species (*H. urceolatum*, *S. cusucoana, S. paulhousei*) were highlighted as being of high conservation concern in their initial descriptions, although to date all remain unassessed by the IUCN. *S. cusucoana* and *C. carolineae* are known solely from a small area in the west of CNP. Given the very small extent of known occurrence for these species, along with alarming deforestation trends in western CNP (see below), it is likely that all these species warrant Endangered or Critically Endangered status.

Surveys in CNP have also made a substantial number of additions to the Honduran flora; these involve major extensions to the known range of some species such as the fern *Serpocaulon lasiopus* (Batke & Hill 2013).

The low number of non-native species in the CNP flora, at least within the well-studied core zone, is striking – and a matter for favourable comment. Only one non-native tree species was recorded as naturalized: *Syzygium jambos* (Rose-apple, family Myrtaceae). A native of south-east Asia, it is widely cultivated in the tropics as a fruit-tree, but in many locations it has become a damaging invasive (Burman *et al.* 2017). Two non-native herbaceous species grown as ornamental garden plants in the region are naturalized in more disturbed forest within CNP: *Crocosmia* x *crocosmiiflora* (Montbretia, family Iridaceae) and *Impatiens walleriana* (Busy Lizzie, family Balsaminaceae).

The bryophyte flora of CNP has received only cursory investigation. Fifteen mosses have been identified (eleven to species level) and ten liverworts (four to species level) (Fundación Ecologista 1994; D.L. Kelly *unpubl. data*). In addition, some ecological studies carried out in the Park have used bryophyte cover as a proxy for microclimate conditions (Batke *et al.* 2015). At lower elevations, bryophytes are plentiful but generally not conspicuous. Even in the pine forests, where bryophyte cover is generally low, hummocks of the bog-moss *Sphagnum meridense* are locally frequent. The bryophyte flora increases in luxuriance and diversity with increasing elevation. In upper montane forest and elfin forest – where the humidity is more or less permanently close to saturation – trunks, branches and logs are swathed by a sward of leafy liverworts, mosses, filmy ferns, lichens and other epiphytes. This sward includes species of *Bazzania*, *Ceratolejeunea, Cheilolejeunea, Herbertus*, and *Lepidozia* — all liverwort genera that are characteristic of neotropical montane rain forest. Another feature of the upper montane zone is the pendant life form: bryophytes that hang down from tree trunks and branches, forming 'streamers' up to 20-40 cm long. This life form is represented in CNP by the mosses *Phyllogonium fulgens*, *Pilotrichella flexilis* and *Isodrepanium lentulum* and the leafy liverwort *Frullania convoluta*.

Ecological studies, particularly related to canopy epiphytes in CNP, have shown that the community structure is particularly influenced by differences in elevation, which correlates with changing vapour pressure deficit and historical wind disturbance from hurricanes (Batke & Kelly 2015). The impact of historical high energy weather events in CNP (e.g. hurricane Mitch in 1998) is most pronounced on south-facing ridges, as confirmed by visible tree impact assessments (Batke & Kelly 2014) and a hurricane impact model (Batke *et al.* 2014).

TABLE 1. Endemic and threatened or near-threatened species in focal taxonomic groups in Cusuco National Park

Group	# species	# endemics (%)	# IUCN threatened (%)
Trees and shrubs	327	167 (49.0)	19 (5.8)
Jewel scarabs	7	7 (100)	0
Dung beetles	40	15 (37.5)	0
Orchid bees	24	4 (16.8)	0
Sphingid moths	63	N/A	0
Saturniid moths	35	N/A	0
Amphibians	30	26 (93.3)	20 (70)
Reptiles	72	46 (63.9)	11 (15.3)
Birds	263	75 (28.5)	11 (4.8)
Mammals	105	22 (21.0)	6 (5.7)
TOTAL	966	362 (37.5)	67 (7.1)

Table 1. Endemic and threatened or near-threatened species in focal taxonomic groups in Cusuco National Park. Endemism refers to species restricted to the Mesoamerican biodiversity hotspot following Myers et al. (2000). Endemism status of moths is in the process of being assessed. Threat status follows IUCN (2020).

TABLE 2. Threatened, near-threatened and data -deficient species occurring in Cusuco National Park.

Class	Order	Common name	*Scientific name*	IUCN status	Trend
Plantae	Pinales	Schwerdtfeger's pine*	*Pinus tecunumanii*	VU	↓
	Magnoliales	Cochrane's magnolia*	*Magnolia cochranei*	EN	?
		Orejuela*	*Cymbopetalum mayanum*	EN	?
	Laurales	Cafecillo*	*Mollinedia butleriana*	CR	?
		Aguacate bajo*	*Persea donnell-smithii*	VU	↓
	Saxifragales	Montón*	*Molinadendron hondurense*	CR	?
	Malpighiales	Meados de burro*	*Gloeospermum boreale*	CR	?
	Fagales	Honduras walnut*	*Alfaroa hondurensis*	VU	?
		Roble de costa*	*Quercus insignis*	EN	?
		Skinner's oak *	*Quercus skinneri*	VU	?
	Sapindales	West Indian cedar	*Cedrela odorata*	VU	↓
	Cornales	Disc-flowered dogwood*	*Cornus disciflora*	VU	?
	Apiales	Mano de león*	*Oreopanax echinops*	VU	?
		Mano de león*	*Oreopanax sanderianus*	VU	?
	Ericales	Cuya*	*Parathesis vulgata*	EN	?
	Arecales	Oblong parlour palm*	*Chamaedorea oblongata*	VU	↓
	Lamiales	Azulito*	*Vitex cooperi*	EN	?
	Caryophyllales	Guatuzo*	*Neea acuminatissima*	EN	?
	Myrtales	Guayabo*	*Terminalia bucidoides*	EN	?

Amphibia	Anura	Robber frog sp. #	*Craugastor charadra*	VU	?
		Coffee rain frog #	*Craugastor coffeus*	CR	↓
		Robber frog sp. #	*Craugastor cyanochthebius*	EN	↓
		Robber frog sp. *	*Craugastor laevissimus*	EN	↓
		Broad-headed rainfrog *	*Craugastor laticeps*	NT	?
		Miles robber frog #	*Craugastor milesi*	CR	?
		Robber frog sp. *	*Craugastor rostralis*	VU	↔
		Copan brook frog #	*Duellmanohyla soralia*	EN	?
		Copan tree frog #	*Ecnomiohyla salvaje*	EN	↓
		Ranita de bromelia pequeña #	*Bromeliohyla melacaena*	EN	↓
		Copan Stream Frog *	*Ptychohyla hypomykter*	VU	↓
		Honduras spike-thumb frog #	*Plectrohyla dasypus*	CR	↓
		Exquisite spike-thumb frog #	*Plectrohyla exquisita*	CR	↓
	Urodela	Salamander sp. #	*Bolitoglossa conanti*	VU	↓
		Salamander sp. #	*Bolitoglossa diaphora*	EN	↓
		Giant palm salamander *	*Bolitoglossa dofleini*	NT	↓
		Dunn's mushroomtongue salamander #	*Bolitoglossa dunni*	EN	?
		Cortes salamander #	*Cryptotriton nasalis*	EN	?
		Salamander sp. #	*Nototriton brodiei*	EN	?
		Worm salamander sp. #	*Oedipina tomasi*	CR	↓

Reptilia	Squamata	Mountain lesser galliwasp #	*Diploglossus montanus*	EN	↓
		Anole sp. #	*Anolis amplisquamosus*	CR	↓
		Cusuco anole #	*Anolis cusuco*	EN	↔
		Stadelman's worm snake*	*Amerotyphlops stadelmani*	VU	?
		Cusuco earth snake #	*Geophis nephodrymus*	VU	↓
		Espinal's coffee snake *	*Ninia espinali*	NT	↓
		Snake sp. #	*Omoadiphas aurula*	VU	↓
		Graceful brown snake sp.#	*Rhadinella pegosalyta*	VU	↓
		Monte cristi graceful brown snake *	*Rhadinella montecristi*	VU	↓
		Cloud forest parrot snake*	*Leptophis modestus*	VU	↓
		March's palm pit viper *	*Bothriechis marchi*	EN	↓
Aves	Tinamiformes	Great tinamou	*Tinamus major*	NT	↓
	Galliformes	Highland guan *	*Penelopina nigra*	VU	↓
		Great curassow	*Crax rubra*	VU	↓
	Accipitriformes	Ornate hawk-eagle	*Spizaetus ornatus*	NT	↓
	Apodiformes	Black swift	*Cypseloides niger*	VU	↓
	Trogoniformes	Resplendent quetzal*	*Pharomachrus moccino*	NT	↓
	Coraciiformes	Keel-billed motmot *	*Electron carinatum*	VU	↓
	Passeriformes	Olive-sided flycatcher	*Contopus cooperi*	NT	↓
		Wood thrush	*Hylocichla mustelina*	NT	↓

		Golden-winged warbler	*Vermivora chrysoptera*	NT	↓
		Golden-cheeked warbler	*Setophaga chrysoparia*	EN	↓
Mammalia	Cingulata	Northern naked-tailed armadillo	*Cabassous centralis*	DD	?
	Eulipotyphla	Omoa broad-clawed shrew#	*Cryptotis mccarthyi*	DD	?
	Cetartiodactyla	Central American red brocket	*Mazama temama*	DD	?
	Perissodactyla	Baird's tapir	*Tapirus bairdii*	EN	↓
	Chiroptera	Van Gelder's bat *	*Bauerus dubiaquercus*	NT	?
		Eastern pipistrelle	*Perimyotis subflavus*	VU	↓
	Carnivora	Jaguar	*Panthera onca*	NT	↓
		Margay	*Leopardus wiedii*	NT	↓
	Primates	Mantled Howler Monkey	*Alouatta palliata*	VU	↓
				Total species	70

Table 2. Threatened, near-threatened and data -deficient species occurring in Cusuco National Park. Status follows IUCN (2020). ↓ = a declining species trend, ↔ = stable trends and ? = unknown trends, * are endemic to the Mesoamerican biodiversity hotspot (Myers et al. 2000), # are micro-endemics known only from the Merendón Mountain range and immediately adjacent areas. DD = Data Deficient, NT = Near Threatened, VU = Vulnerable, EN = Endangered and CR = Critically Endangered. For Plantae, only trees and shrubs were assessed.

TABLE 3. Micro-endemics occurring in Cusuco National Park which are restricted to the Merendón range and immediately adjacent areas. † indicates IUCN (2020) threatened status.

Class	Order	Common name	*Scientific name*
Magnoliopsida	Gentianales	Cusuco coffee tree	*Sommera cusucoana*
	Santalales	Honduras tree	*Hondurodendron urceolatum*
	Ericales	Paul House's snowbell tree	*Styrax paulhousei*
Liliopsida	Arecales	Forked-leaf parlour palm	*Chamaedorea frondosa*
		Molina's parlour palm	*Chamaedorea molinana*
	Zingiberales	Caroline's calathea	*Calathea carolineae*
Clitellata	Haplotaxida	Potworm sp.	*Bryodrilus hondurensis*
		Potworm sp.	*Bryodrilus hondurensis*
Hexanauplia	Cyclopoida	Copepod sp.	*Olmeccyclops hondo*
	Harpacticoida	Copepod sp.	*Moraria catracha*
		Copepod sp.	*Moraria cusuca*
Ostracoda	Podocopida	Seed-shrimp sp.	*Elpidium merendonense*
Arachnidae	Opiliones	Cosmetid sp.	*Eucynorta rooneyi*
	Trombidiformes	Watermite sp.	*Hydrodroma moralesi*
		Watermite sp.	*Flabellifrontipoda triscutata*
		Watermite sp.	*Monatractides angelae*
		Watermite sp.	*Pseudotorrenticola espinasseae*

		Watermite sp.	*Atractides jenniferae*
		Watermite sp.	*Recifella cusucoensis*
Insecta	Coleoptera	Longhorn beetle sp.	*Derobrachus cusucoensis*
		Jewel scarab sp.	*Chrysina cusuquensis*
		Jewel scarab sp.	*Chyysina pastori*
		Jewel scarab sp.	*Chrysina porioni*
		Plant Beetle sp.	*Electribius llamae*
	Diptera	Moth-fly sp.	*Moruseodina cusucoensis*
		Chironomid sp.	*Polypedilum panacu*
Amphibia	Anura	Robber frog sp. †	*Craugastor charadra*
		Coffee rain frog †	*Craugastor coffeus*
		Robber Frog sp. †	*Craugastor cyanochthebius*
		Miles robber frog †	*Craugastor milesi*
		Copan brook frog †	*Duellmanohyla soralia*
		Copan tree frog †	*Ecnomiohyla salvaje*
		Ranita de bromelia pequeña. †	*Bromeliohyla melacaena*
		Honduras spike-thumb frog †	*Plectrohyla dasypus*
		Exquisite spike-thumb frog †	*Plectrohyla exquisita*
	Urodela	Salamander sp. †	*Bolitoglossa conanti*
		Salamander sp. †	*Bolitoglossa diaphora*
		Dunn's mushroomtongue salamander †	*Bolitoglossa dunni*
		Cortes salamander †	*Cryptotriton nasalis*

		Salamander sp. †	*Nototriton brodiei*
		Worm salamander sp. †	*Oedipina tomasi*
Reptilia	Squamata	Mountain lesser galliwasp †	*Diploglossus montanus*
		Anole sp. †	*Anolis amplisquamosus*
		Cusuco anole †	*Anolis cusuco*
		Cusuco earth snake †	*Geophis nephodrymus*
		Snake sp. †	*Omoadiphas aurula*
		Graceful brown snake sp. †	*Rhadinella pegosalyta*
Mammalia	Eulipotyphla	Omoa broad-clawed shrew	*Cryptotis mccarthyi*
		Cruz's Long-tailed Shrew	*Sorex cruzi*
			Total species - 49

Table 3. Micro-endemics occurring in Cusuco National Park which are restricted to the Merendón range and immediately adjacent areas. † indicates IUCN (2020) threatened status. True numbers of micro-endemic plants and invertebrates are likely to be considerably higher than displayed due to lack of study.

Fungi. The first opportunistic fungi survey was completed in CNP in 2019. A total of 93 fungi have thus far been identified to order, 66 to genus and 25 to species-level. Of the fungi examined, 38 were identified as Agaricales (gilled mushrooms), followed by 11 of both Helotiales (cup fungi) and Hypocreales (well-known as insect pathogens). Of the fungi identified to genus level, ten were *Marasmius*, seven *Xylaria*, and five *Amanita*. ITS sequences have been generated and analysed for 18 collections. A BLAST search in NCBI GenBank for ten sequences resulted in 89.05–97.60% identity hits, implying that these collections either represent undescribed species or species that have not yet been sequenced. Given that other studies have highlighted high degrees of fungal endemism in cloud forest ecosystems (Smith *et al.* 2013; Bandala *et al.* 2016; Del Olmo-Ruiz *et al.* 2017), it is likely that there are multiple undescribed species of fungi in CNP. Based on the 2019 fieldwork alone, one new species – a crust-like fungus *Trechispora hondurensis* (*Trechisporales*) – has been described (Haelewaters *et al.* 2020) and additional undescribed species are expected in the following genera: *Chlorociboria*, *Ionomidotis* (Helotiales), *Cyathus*, *Gymnopus*, *Mycena*, *Pterula* (Agaricales), *Mycocitrus* (Hypocreales), and *Xylaria* (Xylariales). In the coming years, a formal fungal ATBI project will be initiated within CNP, which will collect and describe specimens from above-ground ephemeral fruiting bodies of non-lichenized fungi (*sensu* Haelewaters *et al.* 2018). In addition, we also plan to collect fungi associated with arthropods including *Hypocreales* and *Laboulbeniales*; these groups remaining very poorly studied within tropical forest ecosystems (Araújo & Hughes 2016; Blackwell *et al.* 2020).

Arthropods. Comprehensive taxonomic assessment of arthropods is incredibly challenging in tropical forest ecosystems (Basset *et al.* 2012). Major surveys, for which sampling has been sufficient to confidently estimate total species richness, have focused on Scarabaeinae dung beetles, *Chrysina* jewel scarabs, saturnid and sphingid moths, and orchid bees (Euglossini). Sampling of these taxa has been largely a result of the availability of appropriate expertise, as well as the ecosystem importance of the Scarabaeinae. Surveys completed to date have detected 40 species of Scarabaeinae (T. Creedy *et al.*, *unpubl. data*), seven species of *Chrysina* (Jocque *et al.* 2013a; Monzón Sierra & Hawks 2020), 24 species of Euglossini (including two new country records) (McCravy *et al.* 2016), 63 species of Sphingidae (including multiple new country records; Vanhove *et al.* 2012) and 35 species of Saturnidae (S. Waters, *unpubl. data*) (Table 1). All *Chrysina* species, four Euglossini and at least 15 Scarabaeinae are Mesoamerican endemics; endemism status of moth species is in the process of determination. No threatened species from any of these groups have been detected in CNP to date.

Small scale surveys on other groups have also been completed. These have detected 112 ant species (Antweb, 2020), 30 as-yet-undescribed species of Curculionidae and Staphylinidae beetles, all of which are thought to be Park endemics (Anderson & Ashe 2000), and eight species of Cosmetidae harvestmen (Damron 2020) including at least one that is new to science (Damron *et al.* 2018), along with at least 10 morphospecies of other Opiliones families (Damron 2014). Further *ad hoc* collection in CNP has yielded numerous new species discoveries including a large longhorn beetle (Santos-Silva *et al.* 2018), an elateroid beetle (Gimmel & Bocakova 2015), several leaf litter copepods (Fiers & Jocque 2013), and a new mantid genus (Rodrigues *et al.* 2017).

Long-term studies of tank bromeliad systems (Jocque *et al.* 2010) have revealed a high diversity of arthropod species, with high endemism within the chironomids (Mendes *et al.* 2011), oligochaetes (Schmelz *et al.* 2015), and psychodids (Bravo *et al.* 2014). Aquatic bromeliads in CNP have up to seven

species of passively dispersed crustaceans, including at least one endemic seed-shrimp (Pinto & Jocque 2013). This is the highest regional record for phytotelmata biodiversity worldwide (Jocque *et al.* 2013b). Research in CNP has shown phytotelmata invertebrate community diversity to be positively related to bromeliad size (Jocque & Field 2014). Due to their inherent ephemerality, predation and resource use are the main factors structuring phytotelmata communities (Petermann *et al.* 2015; Cereghino *et al.* 2018).

Research into communities of lotic invertebrates in the streams and rivers of CNP indicate that such communities are overwhelmingly dominated by insects (98.5%), and that at least 136 species of 87 families occur, including 15 beetle families, 14 caddisfly families, 14 fly families (O'Callaghan & Kelly-Quinn 2017), and six water mite species (Wiles 2005). Community composition in different river systems is driven by a variety of factors, with elevation and water pH being particularly important (O'Callaghan & Kelly-Quinn 2017).

These data undoubtedly represent just a small fraction of true arthropod diversity in CNP, as evidenced by DNA-based surveys. For example, more than 8,000 operational taxonomic units (OTUs, presumptive species) were uncovered among the 50,000 arthropod specimens individually analysed using DNA barcoding from understorey malaise trap collections across 750 trap-days (D'Souza & Hebert 2018). In the canopy, more than 900 arthropod OTUs were detected in a single tree using metabarcoding (Creedy *et al.* 2019), and over 7,000 from modest sampling of two tree species from four localities in the core zone (Creedy 2018). These results reveal high levels of compositional and phylogenetic turnover in both understory and canopy communities, driven by the elevational gradient and high habitat heterogeneity across the core zone of the park. Overall, these DNA-based studies provide an insight into the high arthropod diversity supported in CNP, a large portion of which await discovery.

Herpetofauna. CNP is acknowledged as an internationally important site for threatened amphibians and reptiles (Le Saout *et al.* 2013; AZE 2018; BirdLife International 2020). A total of 102 species have been found here, included 72 mesoamerican endemics (70.6% of all species) and 31 threatened or near-threatened species (30.4% of all species) (Table 1). These totals include eight micro-endemics known only from CNP, all of which are IUCN listed. These are the Critically Endangered *Anolis amplisquamosus* (McCranie *et al.* 1992), *Plectrohyla dasypus* (McCranie & Wilson 1981), *Plectrohyla exquisita* (McCranie & Wilson 1998), and *Oedipina tomasi* (McCranie 2006a); the Endangered *Bolitoglossa diaphora* (McCranie & Wilson 1995) and *Bromeliohyla melacaena* (McCranie & Castañeda 2006); and the Vulnerable *Rhadinaea pegosalyta* (McCranie 2006b) and *Geophis nephodrymus* (Townsend & Wilson 2006). The Park is also a key stronghold for three further Critically Endangered and Endangered species that are endemic to the Merendón range: *Craugastor coffeus* (McCranie & Köhler 1999; Kolby 2009), *Craugastor milesi* (Kolby & McCranie 2009), and *Ecnomiohyla salvaje* (Solis *et al.* 2017). Ongoing additions of species to the Park's herpetofauna checklist include several snakes (Townsend *et al.* 2005a,b), anoles (Townsend & Plenderleith 2005), salamanders (Townsend *et al.* 2006; Kolby *et al.* 2009), and frogs (Kolby & McCranie 2009). Later additions have generally come from less-studied ecosystem frontiers, such as the tree canopy (Solis *et al.* 2017).

Birds. A total of 263 bird species have been definitively recorded in CNP, comprising 46 different families (S. Jones, *unpubl. data*). At least 24 additional species have been reported, but the authenticity of these records requires confirmation.

Of the recorded bird species, six are classified by the IUCN (2020) as Near Threatened, four as Vulnerable, and one as Endangered (Table 2). A number of the typical highland species of CNP are northern Mesoamerican endemics, such as the Highland Guan (*Penelopina nigra*), White-faced Quail-Dove (*Zentrygon albifacies*), Green-throated Mountain-Gem (*Lamporнis viridipallens*), Emerald-chinned Hummingbird (*Abeillia abeillei*), and Rufous-browed Wren *Troglodytes rufociliatus* (Fagan & Komar 2016). These species, along with several threatened taxa (e.g. Resplendent Quetzal *Pharomachrus moccino* and Keel-billed Motmot *Electron carinatum*; Table 2), are dependent

on intact montane forest, and their abundance in CNP declines away from the core zone of the Park (Martin & Blackburn 2009). Avian richness and diversity patterns inherently decline with increasing elevation (McCain 2009) but, since the initiation of standardized monitoring in 2007, the species composition of CNP has seen upslope shifts in many forest-dependent species, such that species composition at higher elevations has seen increasing influences by species communities typical of lower elevations (Neate-Clegg *et al.* 2018; Neate-Clegg *et al.* under review).

Owing to seasonal timing of our annual fieldwork, the Park's resident avifauna is substantially known (e.g. Martin *et al.* 2016). However, CNP is also a key site for Nearctic migrants (e.g. Komar *et al.* 2011). Approximately 46 migratory species have been recorded in CNP, including three Near Threatened species (Olive-sided Flycatcher *Contopus cooperi*, Golden-winged Warbler *Vermivora chrysoptera*, and Wood Thrush *Hylocichla mustelina*), and one Endangered species (Golden-cheeked Warbler *Setophaga chrysoparia*) (Table 2). The Park is a key site for Golden-cheeked Warbler, the wintering distribution of which is restricted almost entirely to the highland Pine-Oak (*Pinus-Quercus* spp.) forests of Guatemala and Honduras (Groce *et al.* 2010). In contrast to many resident species, however, many of these migrants are capable of utilizing, to a degree, degraded forest and non-forest habitats (e.g. Rappole *et al.* 1999; Wunderle & Latta 2000), such as shade-grown coffee plantations in the buffer zone on the east side of CNP. Feather samples from 11 species of migrant warblers collected during winter fieldwork have also been contributed to the 'genoscape' project (www.birdgenoscape.org), a transnational study examining the breeding origins of declining Nearctic migrant songbirds.

Mammals

There are 46 non-volant mammal species recorded from 26 families in CNP (Table 1); 43 of these are inventoried in Hoskins *et al.* (2018), with the remaining three species being a newly-described species of shrew (*Sorex cruzi*) (Andino-Madrid *et al.* 2020), an as-yet unidentified water mouse (see below), and the Central American Woolly Opossum (*Caluromys derbianus*). A total of 59 bat species from six families have been recorded to date (Medina-Van Berkum *et al.* 2020). Of the 105 mammal species that occur, 22 are Mesoamerican endemics and six are of conservation concern: the Endangered Baird's tapir (*Tapirus bairdii*), the Vulnerable mantled howler monkey (*Alouatta palliata*), and eastern pipistrelle (*Perimyotis subflavus*) and the Near Threatened margay (*Leopardus wiedii*), jaguar (*Panthera onca*), and Van Gelder's bat (*Bauerus dubiaquercus*).

A further three species in CNP are classified as Data Deficient (Table 2). One of these, the Omoa broad-clawed shrew (*Cryptotis mccarthyi*) is one of two micro-endemic mammals (along with the newly described *Sorex cruzi*) restricted entirely to the Merendón range. Given their small geographic range, it is likely both these species will be listed as threatened when sufficient information is available - a trend that is common for range-restricted Data Deficient species (Bland *et al.* 2015). Water mouse (*Rheomys* spp.) specimens have been captured along high-elevation streams - the first records of this genus within Honduras. While they are still to be fully identified, preliminary analyses indicate that their gross external phenotype and skull morphology differ significantly from Thomas's water mouse (*R. thomasi*) and Goldman's water mouse (*R. raptor*), found respectively to the north in Mexico and Guatemala and south-west in El Salvador. Further, it appears the Honduran specimens are more distinct from those species than they are from one another, suggesting a new species, subspecies, or race; molecular genetic analyses are ongoing (N. Reid, *unpubl. data*). Bat surveys have yielded numerous important range extensions, most notably the funnel-eared bat *Natalus lanatus*, which is the second record of this species in Honduras (Medina-Van Berkum *et al.* 2020).

International ecological significance

Biodiversity surveys demonstrate CNP to possess high richness and high endemism, and to support large numbers of globally threatened species in a relatively small area. CNP represents just 0.02% of the total extent of the Mesoamerican biodiversity

hotspot yet supports at least 3.8% of plant species, 16.4% of vertebrate species, and 14.6% of regionally endemic vertebrates found in this hotspot, following species totals given in Myers *et al*. (2000).

The true biodiversity of CNP is inevitably even greater than that summarised above, given the seasonal nature of most fieldwork (e.g. Nearctic migratory birds are likely underrepresented), the many micro-habitats that remain under-surveyed (e.g. the canopy) and the many species that are likely cryptic, both in terms of their ecology and their genetics. Irrespective of these gaps in surveying, the international importance of CNP is shown by its listing as the 123rd most 'irreplaceable' protected area globally (as well as the 48th for threatened taxa and 25th for threatened amphibians) (Le Saout *et al*. 2013) and its designation as a Key Biodiversity Area (BirdLife International 2020) and an Alliance for Zero Extinction site (AZE 2018). The conservation value of CNP additionally extends beyond these biodiversity statistics; it is also important for ecological connectivity on a landscape scale (DeClerck *et al*. 2010). In particular, it represents an important section of the Central American jaguar corridor, facilitating movements between populations in Honduras and populations in Guatemala and Belize (Wultsch *et al*. 2016; Petracca *et al*. 2017). Jaguars remain extremely rare within the Park. Despite a seven-year camera trapping survey carried out throughout the Merendón range by Panthera, only a single photographic record of a jaguar was captured in CNP: a young adult male that remained in the Park´s core zone for over one month in 2016 and was never recorded in the area again (F. Castañeda *et al*., *unpubl. data*). We speculate this could have been a dispersing individual traveling between the established jaguar populations at the Nombre de Dios mountain range in Honduras and the Selva Maya in Guatemala. This points to the importance of small protected areas such as CNP as stepping-stones along the jaguar corridor, providing resting and feeding grounds for traveling individuals, and sustaining landscape-scale connectivity for this large carnivore.

Diversity and endemism in CNP are driven by several factors, including the overlapping of Nearctic and Neotropical species that are characteristic of Mesoamerica (the 'Great American Biotic Interchange' Stehli & Webb 1985; Morrone 2010), and the elevational turnovers and biogeographical isolation inherent to tropical montane forests (Körner & Spehn 2002) which drives both endemism and high beta diversity (Shmida & Wilson 1985). Moreover, CNP has both a Caribbean and a Pacific/inland-facing slope, each possessing different microclimates (Martin *et al*. 2016).

While the ecosystems of CNP are evidently of international significance, it is important to note that high biodiversity and endemism are the rule rather than the exception for tropical cloud forests (e.g. Bruijnzeel *et al*. 2011). Accurately comparing biodiversity between Mesoamerican cloud forests is invariably difficult owing to disparities in survey effort, widely differing sizes and altitudinal ranges, and the geographical attributes of remaining cloud forest fragments (Schuster & Cano 2006). That being said, a comparison of woody plant diversity in CNP with four comparable protected cloud forest areas in Honduras (Table 4), for example, shows broadly similar species richness among four of the five sites (the lower diversity for the Texiguat-El Paraíso site reflects its narrower altitudinal range). Basic comparisons of other taxa from other Mesoamerican cloud forest sites show similar trends. For example, Monte Verde in Costa Rica, perhaps the only other Mesoamerican cloud forest with a comparable intensity and duration of vertebrate monitoring and surveillance effort, has somewhat greater mammal (155 vs 105 species) and herpetofauna (161 vs 102 species) diversity, and substantially greater bird diversity (500 vs 263 species) than CNP (Bermúdez *et al*. 2005; Nadkarni & Wheelwright 2014). Such differences may come about due to Monteverde being larger, more heterogenous (albeit covering a smaller elevational range), further south along the latitudinal diversity gradient, and more intensively studied, with surveys dating back to the 1970s (Nadkarni & Wheelwright 2014). Comparisons of Scarabaeinae dung beetle fauna, meanwhile, suggest CNP to have higher diversity than cloud forest sites in Veracruz, Mexico (Pineda *et al*. 2005), although this is likely due, at least in part, to a sampling bias. The euglossine community in CNP, on the other hand, is less speciose than reported from a Panamanian study site (Ackerman & Roubik 2012); this is most

TABLE 4. Comparisons of woody plant diversity (trees and shrubs identified to a species level) between Cusuco National Park and four other protected Honduran cloud forest sites: Sierra de Agalta, Pico Bonito, El Paraíso, and Uyuca.

Protected Area	Area (km^2)	Altitude (m)	Distance from CNP (km)	# species identified to species level	# species shared with CNP	Sørensen coefficient of similarity between floras	# IUCN-listed threatened species	# IUCN-listed threatened species from that area only
Cusuco National Park (CNP)	234.4	500-2242	NA	327	NA	NA	19	10
Sierra de Agalta	207.9	1800-2354	300	223	82	0.30	8	3
Pico Bonito	564.3	~100-2435	172	291	94	0.30	15	6
Texiguat, El Paraiso	~1,900	1244-1648	270	96	23	0.11	2	0
Uyuca (combined datasets)	5.79	800-2008	242	247	65	0.23	7	1

Table 4. Comparisons of woody plant diversity (trees and shrubs identified to a species level) between Cusuco National Park and four other protected Honduran cloud forest sites: Sierra de Agalta, Pico Bonito, El Paraiso, and Uyuca. Diversity values in these other reserves are based on Pfeifer (1960), House et al. (2006), Carbajal Vásquez (2010), and unpublished data from Zamorano herbarium. Sørensen coefficient values quantify similarity of woody plant community composition between Cusuco National Park and the other four sites. Assessment of threat status (Vulnerable, Endangered or Critically Endangered) is taken from IUCN (2020).

probably a reflection of the smaller elevational range studied in CNP.

Overall, available data indicates that Cusuco is not necessarily exceptional with regards to the number of species found within its borders. It is unique, however, with respect to the community of species it supports. A comparison of the tree and shrub floras of CNP with the four other Honduran cloud forest Protected Areas mentioned above shows CNP to be distinct from all the other sites, as evidenced by the low Sørensen coefficient values (Table 4). Each site also supports different threatened species: only one of a total of 29 IUCN-listed species was recorded from all five sites (Table 4). It seems clear that each Mesoamerican cloud forest site represents its own unique 'island in the sky'. However, the comparison of tree and shrub data shows that sites can be far from equal in overall conservation value. Some had large numbers of threatened species: CNP topped the list, with 19 threatened tree & shrub species, of which ten were not recorded from any of the other sites. This was independent of site size (e.g. Pico Bonito National Park was second to CNP despite being more than twice the size) (Table 4).

2.3. Ecosystem services

In addition to its biodiversity value, CNP also provides a wide range of the ecosystem services. Perhaps most significantly, the Park forms part of the watershed for the city of San Pedro Sula and parts of the Greater Sula Valley, providing clean water as well as flood and soil erosion prevention services to *ca.* 800,000 people (www.citypopulation.de). Indeed, safeguarding this part of the Merendón water catchment was the principal reason CNP was initially designated a protected area.

A further key service provided by CNP is carbon sequestration. Cloud forests, due to their small extent, fragmented nature, and steep topography, do not generally store as much carbon as intact lowland tropical forest ecosystems (e.g. Martin *et al.* 2015). Nonetheless, they are regionally still important carbon reservoirs (Leija-Loredo *et al.* 2018). Neotropical montane forests contain on average 123.5 MgC/ha (megagrams of carbon per hectare) aboveground (Spracklen & Righelato, 2014) with a further 25% (30.9 MgC/ha) belowground (Cairns *et al.* 1997), yielding a total standing stock of 154.4 MgC/ha. In 2000, CNP was estimated to be 94% forested with 22,790 ha of extant forest (Hoskins 2019). Derived from these figures, a preliminary baseline estimate might suggest the Parks' ecosystems sequestered 3.5 million MgC in 2000.

3. Environmental threats, stresses, and contributing factors

Despite its high biological importance, CNP faces a range of environmental threats, driven by various contributing factors, which have led to stresses such as habitat loss, severe defaunation, and release of greenhouse gases (Salafsky *et al.* 2008). The four most acute threats facing CNP are deforestation, poaching, disease, and climate change (Fig. 3). We discuss the extent and consequences of each of these threats in turn.

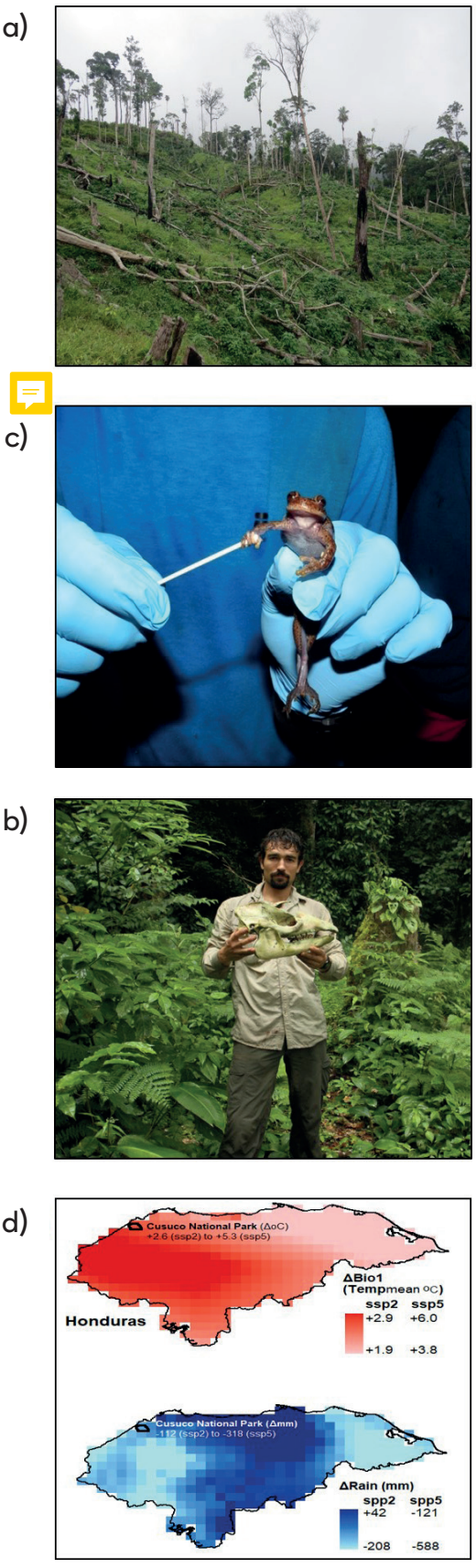

Fig. 3. The four principal environmental threats in Cusuco National Park: deforestation, poaching, disease, and climate change. A) Recent deforestation photographed in July 2019 in the western section of the Park's core zone. B) The skull of a recently poached Baird's tapir (Tapirus bairdii) found in CNP. C) A frog being swabbed for PCR detection of Batrachochytrium dendrobatidis (chytrid fungus) the causative agent of Chytridiomycosis. D) Predicted climate change throughout Honduras highlighting Cusuco National Park in mean temperature in oC and total rainfall in mm between the averages for 1970–2000 and 2081–2100, using the 6th Model for Interdisciplinary Research on Climate (MIROC6) assuming Shared Socioeconomic Pathways SSP2 (the 'Middle of the Road' scenario) and SSP5 ('Fossil-fueled Development' scenario) using 100 grid cells [data extracted from https://worldclim.org].

3.1. Deforestation and habitat degradation

Threats driving habitat loss within cloud forest ecosystems include conversion to agricultural land and livestock grazing, timber extraction, and infrastructural (road and village) development (Aldrich *et al.* 1997; Bubb *et al.* 2004). These have a range of negative impacts which have been associated with tropical deforestation generally (e.g. Harris *et al.* 2012; Alroy 2017), although many of these impacts are exacerbated in cloud forests because they tend to be spatially restricted and highly fragmented (Cayuela *et al.* 2006a; Toledo-Aceves *et al.* 2011).

Honduras possesses one of the highest deforestation rates of any Central American country (Magrin *et al.* 2014), and one of the worst rates globally for deforestation in protected areas (Hansen *et al.* 2020). Analysis of satellite imagery (following Hansen *et al.* 2013) suggests CNP lost >7% (ca. 1,759 ha) of forest from 2000 to 2017, with an average annual loss of 103 ± 99 ha (Hoskins 2019). Annual deforestation rates were highly variable during this period, but worse in recent years (e.g. 2016 and 2017), suggesting this threat is accelerating. Adopting average aboveground carbon stock values from Spracklen & Righelato (2014), we estimate that since 2000 around 217,237 MgC have been released into the atmosphere due to forest loss in CNP (approx. 6.2% of the total carbon store). This is a conservative estimate and does not include releases from belowground carbon stores because the rate of their loss to the atmosphere remains unknown, as does the extent to which replacement agricultural soils act as net carbon sources. The cumulative trend in forest loss has been increasing at a nearly linear rate, with models predicting a doubling of the area deforested (and atmospheric carbon enrichment) over the next 20 years if no effective conservation actions are implemented (Hoskins 2019).

Contributing factors driving habitat conversion in CNP are primarily agricultural, involving the planting of both subsistence crops such as maize and beans, cash-crops such as coffee (the most significant crop on deforested land, at least where favourable conditions occur) and cardamom, and cattle farming. Small-scale marijuana cultivation also occurs in more remote clearings within the Park. The actors associated with the contributing factors of this deforestation range from local subsistence farmers to wealthy individuals financing land clearance and subsequent agricultural development. While reasons for deforestation are broadly similar throughout CNP, patterns of habitat loss are not (Figure 2). In recent years deforestation has been much more pronounced in the northern and western sections of the Park (Fig. 3a), rather than the south and east. The contributing factors driving this disparity are complex. More remote regions of CNP (particularly the western side of the park) are further from central authority in San Pedro Sula and lack a permanent military presence and regular community ranger patrols (see section 4.1), both of which are present in the east, and thus illegal land clearance is more common. Specifically, deforestation on the northern and western slopes of the park may be seen as of less concern because run-off flows directly into the Caribbean Sea rather than into the heavily populated Sula valley (which relies on forest cover for clean water and flood protection). At present, pristine, closed canopy forest in the less protected northwest of CNP's buffer zone, particularly in areas of flatter topography and in proximity to other recently deforested areas, are at greatest risk of forest loss (Figure 2) (Hoskins 2019).

As a result of land conversion, nutrient and sediment run-off have been shown to act as a stressor on the richness and abundance of freshwater macroinvertebrates in small streams in CNP (O'Callaghan *et al.* 2015), although the catchment-scale impacts of this run-off remain unevaluated..

3.2. Poaching

Unsustainable hunting of large vertebrates has been identified as a key threat to biodiversity globally (Maxwell *et al.* 2016) and has been particularly severe in the neotropics (WWF 2018). Additionally, cloud forest ecosystems may be disproportionately impacted by hunting. This is because populations of large-bodied species here tend to be biogeographically isolated in small, genetically depauperate populations with limited immigration to help re-colonization after local extirpation (Brown &

Kodric-Brown 1977). Moreover, small habitat patches are more easily accessible to poachers (Bubb *et al.* 2004). The collapse of large-bodied vertebrate populations in cloud forest ecosystems is a matter of great concern, as these populations are associated with key ecosystem services such as seed dispersal and nutrient cycling (Jones & Safi 2011). Forest carbon sequestration rates have also been associated with mammalian species richness and abundance (Osuri *et al*., 2016).

Community ranger patrols run between 2005 and 2020 (see section 4.1) have logged 147 events corresponding to evidence of poaching in CNP. Most of these events involved the identification of hunting blinds (tapescos in Spanish); a wooden platform constructed high in the trees and used specially to target paca (*Cuniculus paca*). Other poaching evidence includes bullet shells, hunting camp remains, and carcasses.

Analysis of mammalian tracks and signs on standardised transects surveyed annually from 2010 to 2018, adjusted for survey effort, suggests the relative abundance of all terrestrial mammals in CNP has declined by 7% per year on average, with most rapid declines in the Park's more accessible and less rigorously protected buffer zone (Hoskins *et al.* 2020). The Park was once regarded as a Honduran stronghold of the Baird's tapir (McCann *et al.* 2012; McCann 2015), yet recent work suggests it is approaching extirpation from CNP due to poaching (Fig. 3b) and habitat degradation (Hoskins *et al.* 2020). It might be expected that large hunted species (e.g. deer) would exhibit more rapid declines than unhunted species (e.g. wild cats, mustelids etc.). However, even the latter have declined by 6% per year (Hoskins *et al.* 2020), suggesting other threats, such as deforestation and disturbance, are of comparable importance as stressors of population change. Such is the rapidity of observed population declines that it is estimated that populations of many large-bodied mammals in CNP could become functionally extinct as early as the mid-2020s (Hoskins *et al.* 2020).

3.3. Amphibian diseases

Chytridiomycosis is an infectious disease of amphibians caused by the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*). It has caused population declines in over 500 species, with nearly 100 species driven to extinction, and as such is responsible for greater biodiversity loss than any other disease in recorded history (Scheele *et al.* 2019; Fisher & Garner 2020).

Bd has been reported from numerous localities in Honduras (Puschendorf *et al.* 2006; Gutsche *et al.* 2015), including CNP where it was first detected in 2007 (Kolby *et al.* 2010). Retrospective analysis of archived museum material confirmed the presence of chytrid in CNP as early as 1996 (Kolby & Padgett-Flohr 2009), and thus it is likely this pathogen arrived in the region during the early 1990s, if not earlier. Five *Bd* prevalence datasets derived from amphibian swabbing (Fig. 3c) have been analysed. Using PCR analyses, Kolby *et al.* (2009) reported an overall *Bd* prevalence rate of 44.4% from a sample of 257 amphibians of 16 species swabbed in 2007, with certain life-stage groups exhibiting much higher rates (96.2% in juveniles of the Critically Endangered *Plectrohyla dasypus*, N = 27). Clake (2015), using qPCR analyses, reported an overall *Bd* prevalence rate of 19.5% from 848 individuals of four species swabbed between 2011–2014, with highest prevalence rates (31%) being reported in *Ptychohyla hypomykter* (N = 102). Kolby *et al.* (2015b) reported an overall prevalence of 88.5% (N = 52) among juvenile frogs of four species threatened with extinction using qPCR analysis of skin swabs. Blooi *et al.* (2017) reported a prevalence rate of 12.7% in stream-dwelling amphibians (N = 150) and 3.4% in bromeliad-dwelling amphibians (N = 116) from qPCR analysis of swabs collected in 2014 and 2015. A further collection of 80 swabs analysed using qPCR analyses in 2017 reported an overall *Bd* prevalence rate of 57.5%, rising to 64.7% in *P. dasypus* (N = 34) and 100% in *P. hypomykter* (N = 4) (C. Phipps, *unpubl. data*). These data show prevalence rates to be generally high, but variable between species and years. Contributing factors driving this are likely to be, respectively, species' ecology (Blooi *et al.* 2017) and annual variability in rainfall and water availability (Clake 2015; Ruggeri *et al.* 2018).

Samples of chytrid collected from CNP belong to at least two divergent chytrid lineages. Of 20 samples where the lineage could be confirmed, 18 were comprised of the globally distributed hypervirulent *Bd*GPL lineage, and the other two samples

were found to be the *Bd*Cape lineage, apparently endemic to Africa (Byrne *et al.* 2019). These data are noteworthy as they represent the first known presence of *Bd*Cape in the western hemisphere. How *Bd*Cape was introduced to CNP is unclear and warrants further investigation. Regardless, the presence of *Bd*Cape in CNP is a cause for concern, because it presents the opportunity for the generation of highly virulent hybridized strains. Although *Bd* is most often clonal, the phenomenon of sexual recombination was confirmed in Brazil between *Bd*GPL and *Bd*Brazil (Schloegel *et al.* 2012), with the offspring expressing greater virulence towards native amphibians than either of the parental strains (Greenspan *et al.* 2018).

Bd is ubiquitous in CNP and has been detected in nearly all locations where extensive sampling has been completed and where suitable hosts were found. Detection of *Bd* in both rainwater (Kolby *et al.* 2015a) and on the surfaces of vegetation (Kolby *et al.* 2015b) shows how easily it can disperse across the landscape and be transmitted when susceptible amphibians encounter viable spores. A diverse range of amphibians have tested positive for infection, spanning genera that include stream, epiphyte, and canopy-dwelling specialists (Kolby *et al.* 2010; Blooi *et al.* 2017; Thorp *et al.* 2019), although more research is needed to establish whether they all develop the disease chytridiomycosis. Interestingly, results in CNP suggest that bromeliads may represent refugia for certain species as the prevalence rate reported in phytotelmic microhabitats by Blooi *et al.* (2017) was five times lower than in nearby stream habitats. A possible explanation could be due to the low pH of bromeliad water (Jocque & Kolby 2012) or the ability of micro-eukaryotes to ingest chytrid zoospores present in bromeliad tanks (Blooi *et al.* 2017). Interpretation of these findings should, however, be treated with caution, for two reasons. Firstly, while some studies have reported similar results (Lindquist *et al.* 2011), others have demonstrated high *Bd* spore loads and high rates of *Bd* infections within phytotelmata, both in lowland forests (McCracken *et al.* 2009) and cloud forests (Cossell & Lindquist 2009). Secondly, *Bd*-associated mortality rates of amphibians utilizing phytotelmic microhabitats in CNP – which can be very different from chytrid infection rates – have not yet been examined. Further research is therefore necessary before conclusions can be drawn, although it is encouraging to see lower amounts of *Bd* in these arboreal habitats.

Overall, chytridiomycosis represents a critical threat to amphibians throughout CNP, and it may also threaten other species. Amphibian population collapses have knock-on effects on their predators, notably amphibian-feeding snakes (Zipkin *et al.* 2020). In CNP this may impact on species such as the range-restricted Palm viper *Bothriechis marchi*, a frog-eating specialist. A critical avenue for further research is the quantification of temporal population fluxes among threatened amphibians, and the consequences for predator-prey dynamics.

3.4. Climate change

Cloud forests occupy narrow high-elevation climatic niches typified by high rainfall. As such, they are disproportionately impacted by global climate change (Williams *et al.* 2003). Global warming has been shown to cause upslope shifts in species ranges, where the combined effects of competition, shifting habitat boundaries, and shifts in climate envelopes cause mountain top extirpations; the 'escalator to extinction' scenario (Fadrique *et al.* 2018; Freeman *et al.* 2018).

Climate modelling forecasts CNP to be particularly at risk within Honduras, with a 2.6 °C increase in mean annual temperature (from 23.0 °C to 25.6 °C) and a 112 mm decrease in total annual rainfall (from 1,785 mm to 1,673 mm) predicted by the end of the century (2081–2100) in comparison to historical average conditions (1970–2000) (Fig. 3d). These results are based on climate data downloaded from WorldClim (Fick & Hijmans 2017) and the MIROC6 climate model (Tatebe *et al.* 2019) and assume modest projections of global socioeconomic change (i.e. the Shared Socioeconomic Pathway 2, SSP2) (Riahi *et al.* 2017). The most extreme projections (SSP5) suggests that the mean temperature of the park could rise by 5.3 °C with a 318 mm decrease in annual rainfall (Fig. 3d). This increase in temperature will increase evaporation which, together with the expected decreases in precipitation, is predicted to reduce water inflow into Honduran reservoirs by

up to 20% (Maurer *et al.* 2009). Honduras has experienced increasingly frequent and prolonged droughts in recent decades (Rauscher *et al.* 2008) resulting in soil moisture deficits and failures of both subsistence and cash crops (Bunn *et al.* 2018; Calvo-Solano *et al.* 2018). Such stochastic events are likely to cause even more extreme peaks in future temperatures, and more impactful droughts. This is likely to have serious socio-economic consequences, with both climate change and ongoing deforestation likely to have negative impacts on the water provisioning capacity of the Park, as well as its ecological communities.

Montane specialist species are and will be particularly stressed by climate change, either as a direct result of warming on species' thermal physiology (see Polato *et al.* 2018) or as a result of the multiple drivers of habitat loss, interspecific competition, and shifting ecotones that favour lower-altitude generalist species (Jankowski *et al.* 2012). Arthropods inhabiting the rainforest canopy, unprotected by the buffering effect of overhead vegetation, are likely to be affected more acutely by climate change (Nakamura *et al.* 2017). Strong community partitioning and phylogenetic structure among canopy arthropods across small scales (<3 km) in elevational climatic zones in CNP (Creedy 2018) suggests this portion of the Park's fauna are particularly vulnerable to the 'escalator to extinction' effect (Freeman *et al.* 2018). Strong community partitioning patterns have also been observed in CNPs bird community (Jones *et al.* 2020a) and may be similarly vulnerable to this effect.

Upslope shifts in the bird communities of CNP over a ten year period from 2007–2016 have been documented, with elevational shifts consistent across all habitats and also only those in closed-canopy primary forest that had seen no land conversion over that period (Neate-Clegg *et al.* 2018; Neate-Clegg *et al.* under review). These results suggest that elevational upslope shifts in the avian community are being driven primarily by climate change. At present this is the only quantitative assessment of the effects of climate on species communities in the Park; analyses are currently underway utilising the strength of standardised and repeated cross-taxon study.

A final consequence of climate change may be an increase in the frequency and intensity of Caribbean hurricanes (Knutson *et al.* 2010) which may have long-lasting impacts on community composition and vegetation structure in Mesoamerican cloud forests (Tejeda Cruz & Sutherland 2005; Batke & Kelly 2015). Additionally, stronger and more frequent hurricanes may also destroy park infrastructure, making cloud forest protected areas more difficult to manage, and also damage livelihoods in communities surrounding these protected areas, making people more reliant on illegal resource extraction. Both these factors could indirectly threaten the integrity of Mesoamerican cloud forest ecosystems. At the time of writing, CNP had just experienced what is believed to be its most destructive hurricane season in decades, with a category 4 and a category 5 storm causing widespread tree damage, landslides, and destruction of property. The short-term and long-term consequences of these hurricanes will be empirically assessed in future research seasons.

4. Conservation actions

The high biodiversity value of CNP, coupled with the urgency of the environmental threats and associated stresses it faces, have led to a range of conservation actions, which we detail in turn below.

4.1. Community ranger patrols

In August 2012 the Honduran Minister of Natural Resources and Environment directed military personnel to patrol CNP. These patrols used locally hired guides and were employed as a deterrent against the threats of illegal deforestation and poaching. These patrols were *ad hoc* and no data were collected on their efficacy, although some illegal activities were directly disrupted (F. Castaneda, *pers. comm.*). In August 2015, the Jaguares de Cusuco Community Ranger Team was formally established with financial support from Panthera and the Wallacea Trust, and this team have since been carrying out regular patrols in CNP. These rangers patrol using GPS devices, and collect data (e.g. direct observation of poachers, discovery of hunting platforms or poached carcasses) using SMART conservation soft-

ware (https://smartconservationtools.org). At the time of writing, the SMART database included data on 425 patrols (representing a total of 6,108 km walked) completed between 2015 and 2020. These patrols were focussed towards the southern and eastern parts of the Park due to the increased risk of patrolling in the more remote western and northern sections of CNP. Vegetation in two recently deforested areas are regenerating with no further signs of deforestation after being patrolled intensively following initial detection, indicating the value of this conservation action as a deterrent.

Prior to the instigation of the community ranger programme, deforestation would often go undetected for long periods, giving loggers time to build permanent structures (fences, outbuildings, and even houses) on the cleared patches. Honduran law offers certain rights to squatters who have built infrastructure, even on illegally occupied ground. Early detection of deforestation events is therefore highly important, and the community ranger programme offers an effective way to achieve this.

Rangers also log illegal poaching and have recorded 147 incidences so far (see section 3.2.), mostly related to Least Concern species such as lowland paca (*Cuniculus paca*) and white-tailed deer (*Odocoileus virginianus*), although evidence of poaching Endangered species, including the Baird's tapir, has also been recorded. A passive acoustic monitoring survey was also started by Panthera in 2018, with support from the U.S. Fish and Wildlife Service, to monitor poaching activity indirectly. Percussion detection devices have been positioned in trees around CNP to record frequency, timing, and approximate location of gunshots fired in the Park. This acoustic survey is helping to quantify poaching activity in CNP and will play a central role in optimising anti-poaching patrolling calendars. Preliminary results indicate that poaching events are negatively correlated with the temporal and spatial distribution of patrols, as well as with the presence of the annual Operation Wallacea expedition season (F. Castañeda *et al.*, *unpubl. data*). The main limitation of the programme to date is its lack of coverage across the whole of CNP; a substantial issue given that the most extensive deforestation occurs in areas where at present it is difficult for rangers to operate.

4.2. *Ex-situ* captive breeding for reintroduction

Ex-situ conservation methods are often a highly feasible conservation action for amphibians given that they are generally relatively inexpensive to maintain, often breed quickly and in high numbers, and tend to cope physiologically and behaviourally with captive conditions better than larger-bodied taxa (Bloxam & Tonge 1995; Balmford *et al.* 1996). Proof of success for the captive breeding model for amphibians can be seen in the numerous species saved from extinction by *ex-situ* measures (e.g. Dreitz 2006; Lee *et al.* 2006). The number of amphibian species held *ex-situ* in the face of the unfolding amphibian extinction crisis is rapidly growing, both in zoos and smaller 'non-traditional' facilities such as private breeding centres (Biega *et al.* 2017). Facilities located in the country where the captively bred species originate are particularly desirable, given the opportunities for greater engagement with local stakeholders, prevention of disease transmission, better integration of *ex-situ* and *in-situ* strategies, and avoidance of entanglement with restrictive legislation on international movements of wildlife (Martin *et al.* 2014; Biega *et al.* 2017).

One such private breeding facility, the Honduras Amphibian Rescue and Conservation Centre (HARCC 2020), is being developed at Lancetilla Botanical Garden, approximately 70 km to the north-east of CNP. The goal of this centre is to perform head-start and reintroduction activities to prevent the chytrid-driven extinction of three of CNP's threatened and endemic amphibian species: *Plectrohyla dasypus*, *Plectrohyla exquisita*, and *Duellmanohyla soralia*. To help these populations persist in the wild, HARCC's main objective is to collect young frogs from CNP before they die from chytridiomycosis, care for them at the biosecure HARCC research facility, and then reintroduce them back into CNP as healthy adult frogs. A captive assurance programme will also be developed to maintain a breeding population of frogs at HARCC so that animals can continue to be released back into CNP even in the case of a sudden extinction event in the wild. To date, the necessary infrastructure for HARCC has

been completed, but official permission has yet to be provided for the transfer of frogs from CNP to begin. These delays are cause for concern, given the severe stresses amphibians in CNP are facing, and the small window of time that may be available to develop conservation actions to protect them from extinction.

4.3. Ecotourism

Ecotourism has long been highlighted as a means to conserve biodiversity by placing an economic value on keeping ecosystems undisturbed (Boo 1990) and enhancing management capacity building for protected areas (Yu *et al.* 1997). It is often the case that locations which are hotspots for ecotourism are not correlated with sites experiencing high threat, nor those which support high concentrations of endemic species (Kruger 2005). However, CNP (which has both of these attributes) would, in theory at least, be well-placed to benefit from both domestic and international tourism based both on its conservation need and its proximity to San Pedro Sula and its international airport.

To date, tourism in CNP (and in most of Honduras) remains limited. The single biggest source of visitors to the Park is the Opwall research programme, which has brought an average of 350 students and 70 scientists to CNP yearly over the period 2004-2019. As well as paying park fees, these visitors provide seasonal employment for approximately 90 people from surrounding communities as guides, cooks, porters, and other logistical staff. The programme (which is only able to draw visitors due to CNP's exceptional biodiversity) thus generates important revenue for the Park authorities and provides income streams to local communities, albeit for a limited part of the year and for a limited selection of communities. There is also some circumstantial evidence to suggest that the presence of sizeable numbers of visitors in the forest during the Opwall season acts as an active deterrent to illegal activities in CNP. While many of the Opwall long-term survey plots have been deforested in the last 16 years, particularly in the western half of the Park, such deforestation seldom occurs in the June-August period while the expedition is running. Similarly, preliminary acoustic data indicate that poaching events diminish during the Opwall research season (see section 4.1).

As well as conspicuous benefits, it is important to note that visitors to CNP may also have unintended consequences. Camera trap data from CNP have shown that detection rates of hunted large-bodied mammals (deer, peccaries, etc) are highest further from forest camps, presumably due to these species avoiding human disturbance (Hoskins 2019). Camera trap detection of unhunted mammals (e.g. wild cats, mustelids etc.) is highest further from forest trails (which are maintained by annual clearing with a machete and are subject to high daily human traffic during the Opwall season). Care must thus be taken to manage the anthropogenic impacts of large visitor groups so as to minimise negative stresses on wildlife.

One of the biggest challenges in channelling the positive aspects of ecotourism to achieve conservation is ensuring involvement of as many communities as possible. Again, in this respect communities in the northern and western parts of CNP benefit less from ecotourism activities than elsewhere. While the Operation Wallacea programme is not large enough to achieve involvement in all of CNP's communities, finding means to extend other ecotourism ventures elsewhere would be a valuable step.

4.4. Urgent call for conservation and management actions

Despite the implementation of various conservation actions, illegal deforestation and poaching continue in CNP at an alarming rate, indicating that these interventions alone are insufficient to arrest these trends. Theoretically, the status of CNP as a formal protected area should by itself be sufficient to protect against deforestation and poaching threats, but in practice this is not so. Deforestation within protected areas is widespread in the Neotropics (e.g. Bonham *et al.* 2008) and is a particularly acute problem in Honduras (Hansen *et al.* 2020). Funding for CNP is extremely limited, and the capacity of official bodies to effectively monitor and prevent illegal activities is severely restricted. In some other Honduran protected areas co-management agreements between ICF and local communities have been developed to partially offset the lack of centralized

funds supporting conservation actions (ICF 2010). However, at present CNP has no such arrangement. Conservation action in CNP is further complicated by the lack of clear park borders, resulting in ambiguity around the legality of some deforestation and hunting activities. Furthermore, arresting and prosecuting lawbreakers in national parks is potentially dangerous across much of Central America (as demonstrated in the difficulties of organizing community patrols in certain parts of the Park). As such, legislative enforcement and prosecution of illegal activities are somewhat limited in Honduras. This, coupled with the socioeconomic contributing factors of many of these threats, means that actions which entirely focus on prosecution or enforcement may not bring positive change to CNP.

A more holistic approach to conservation - that involves protection enforcement alongside sustainable resource management, while taking social and political contributing factors into account – may offer a more bespoke and positive way forward to resolving environmental issues in CNP (Redford *et al.* 2006). Efficient resolution of human-natural ecosystem conflicts is based on a thorough socio-economic and cultural understanding of the situation and typically requires a multi-dimensional approach, often involving education and awareness programmes, both of which require time. However, rates of habitat loss and poaching in CNP are such that little time remains to prevent irrevocable damage. An intensification of conservation actions is therefore urgently needed in the short term, coupled with a need for more long-term socio-economic strategies. We identify a series of urgent short-term and longer-term conservation actions which need to be implemented in order to safeguard the future of the Park. The successful implementation of these will reduce environmental stresses within CNP by targeting the threats that create these stresses.

Urgent short-term conservation actions:

1) Achieve the compliance and enforcement of environmental regulations within CNP by:

a) Recognizing and communicating precise park borders. Achieving official recognition of the extended delineation of CNP as defined by Corporación Hondureña de Desarrollo Forestal (COHDEFOR) in the park management plan published in 1994, with a subsequent clear communication of these borders (and the legal consequences of infringing them) delivered to surrounding communities, would remove ambiguity about the legality of deforestation and hunting within the area.

b) Expanding the spatial and temporal coverage of community ranger patrols. Anecdotally, patrols appear to be a strong deterrent to poaching in the vicinity of Buenos Aires village on the eastern side of the Park. Most of the community rangers live in this village, and it is likely that a resident ranger presence based in other settlements would also discourage local poaching A higher frequency of patrols throughout the year would also improve their effectiveness.

c) Improving government and military responses. It is vital that authorities respond in a timely manner to information on illegal activities provided by the community rangers, and that the judiciary receive dedicated training to ensure that appropriate sanctions are handed out to the perpetrators of these crimes in accordance with Honduran law. The establishment of a permanent ICF presence within the Park would be a strong step towards facilitating swift responses to illegal activities in CNP.

2) Safeguard threatened species which are declining due to disease by:

a) Conducting species-specific rescue actions. Given the number of threatened micro-endemics in CNP, species-specific conservation

actions will play an important role in averting extinctions. A notable example is the proposed HARCC *ex-situ* conservation facility.

Long-term conservation objectives:

1) Achieve long-term sustainable resource use in the communities surrounding CNP by:

a) Completing extensive social science surveys in communities surrounding the Park. A fundamental first step in achieving long-term sustainable resource use in CNP is to develop a detailed understanding of the drivers and usership of resources and the economics thereof in the communities surrounding the Park. Social science data providing this information is vital with respect to ensuring the success of the actions listed in points b,c,d and e below (Dayer *et al.* 2020).

b) Developing alternative sustainable livelihoods for communities. Providing communities currently dependent on income generated from illegal activities within CNP boundaries with alternative incomes equal or greater to those derived from such activities would, where feasible, reduce economic incentives to deforest and poach. Initiatives could include; nursery plantations and subsequent reforestation for internationally funded carbon sequestration projects; more efficient agriculture in the buffer zone; ecotourism; sustainable harvesting of forest resources; and development of value-added products placed in both domestic and international markets. Such projects would provide a better balance between biodiversity, the services provided by the ecosystem, and the economic well-being of the people who live in and around the Park (Kremen & Merenlander 2018).

c) Establishing a co-management framework that boosts stakeholder participation in CNP. This will allow members of local communities (often represented by local authorities such as water boards and town boards – 'patronatos'), non-governmental institutions, civilians, and national government to work together for the management of CNP, and would enhance the effectiveness of many of the other conservation actions listed here.

d) Developing education and training. Such programmes would empower local communities with the skills, knowledge, and confidence to engage in sustainable local resource management and raise environmental awareness. These would seek to achieve a mentality change and would involve communications with all the communities in and around CNP.

e) Boosting ecologically sensitive ecotourism. Ecotourism, if correctly developed, could provide an important source of income for local communities and a revenue stream for the management of CNP, as well as raise awareness of its conservation value. Links with Honduran schools, universities and other key institutions are essential. There already seems to be a growing number of visitors from an increasingly affluent San Pedro Sula. Avitourism is likely to be an effective means of attracting international visitors; the rich bird community and numerous regional endemics are potentially a strong draw to what has become a lucrative international industry. It is vital for any tourism development in CNP to be conducted in a responsible manner so as to avoid negative impacts on wildlife. Better economic management of tourism in CNP is also necessary. For example, at present there is no effective means of collecting entry fees from tourists, but this could be rectified by placing manned toll booths at entry points to the Park or within the Parks communities.

2) Achieve a better long-term understanding of ecological trends and threat impacts in CNP by:

a) Expanding biodiversity and ecosystem research and monitoring. While the ecology of certain species and ecosystems in CNP are

relatively well-known, many remain unstudied. An expanded research programme, alongside the continuation of existing monitoring, would allow for a more holistic understanding of diversity, endemism, threats, and stresses within the Park. Longer-term datasets would allow for a greater understanding of how certain threats impact the ecology of cloud forest ecosystems (e.g. climate change), and therefore enable more effective monitoring strategies for various taxa. Completing IUCN threat assessments for as-yet-unassessed micro-endemics is also a priority.

Conclusions

This review demonstrates CNP to be of exceptional ecological importance. However, despite its status as a protected area, it remains highly threatened by deforestation, poaching, disease, and climate change. There is some evidence that current conservation actions may mitigate some of these threats. However, these are not sufficient to secure the integrity of CNP's ecosystems, which continue to be degraded rapidly. Urgent short-term conservation actions relating to enforcement, deterrents, and species rescues are required, alongside a suite of interventions and research addressing and understanding underlying socio-economic dynamics in the Park in the longer term, to limit the impacts of deforestation and poaching. Amphibian disease and climate change are harder to manage at local levels and require multi-faceted responses from the international community, although *ex-situ* conservation actions and reforestation projects represent two partial means of mitigating these respective threats. Without immediate implementation of these conservation actions, it is highly likely that the unique cloud forest ecosystem of CNP will experience species extinctions and extirpations, and severe loss of ecosystem services, in the coming decades.

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